



Nesting Success in Crimson Finches: Chance or Choice?

Catherine M. Young, Kristal E. Cain, Nina Svedin, Patricia R. Y. Backwell & Sarah R. Pryke

Division of Ecology, Evolution and Genetics, Research School of Biology, The Australian National University, Acton, Canberra, ACT, Australia

Correspondence

Catherine M. Young, Division of Ecology, Evolution and Genetics, Research School of Biology, The Australian National University, Building 44 Daley Road, Acton, Canberra ACT 2601, Australia.

E-mail: catherine.young@anu.edu.au

Received: May 6, 2015

Initial acceptance: June 19, 2015

Final acceptance: July 22, 2015

(L. Fusani)

doi: 10.1111/eth.12422

Keywords: nest predation, nest defence, nest-site, breeding success

Abstract

In avian systems, nest predation is one of the most significant influences on reproductive success. Selection for mechanisms and behaviours to minimise predation rates should be favoured. To avoid predation, breeding birds can often deter predators through active nest defence or by modifying behaviours around the nest (e.g. reducing feeding rates and vocalisations). Birds might also benefit from concealing nests or placing them in inaccessible locations. The relative importance of these strategies (behaviour vs. site selection) can be difficult to disentangle and may differ according to life history. Tropical birds are thought to experience higher rates of predation than temperate birds and invest less energy in nest defence. We monitored a population of crimson finches (*Neochmia phaeton*), in the Australian tropics, over two breeding seasons. We found no relationship between adult nest defence behaviour (towards a model reptile predator) and the likelihood of nest success. However, nest success was strongly related to the visibility of the nest and the structure of the vegetation. We found no evidence that adult nest building decisions were influenced by predation risk; individuals that re-nested after a predation event did not build their nest in a more concealed location. Therefore, predator avoidance, and hence nest success, appears to be largely due to chance rather than due to the behaviour of the birds or their choice of nesting sites. To escape high predation pressures, multiple nesting attempts both within and between seasons may be necessary to increase reproductive success. Alternatively, birds may be limited in their nest-site options; that is, high-quality individuals dominate quality nest sites.

Introduction

Predation is the most significant cause of nest failure for most passerine birds (Ricklefs 1969; Martin & Cl Robertson 1996). Breeding birds should be able to assess and respond to predation risk (reviewed by Lima 2009) as behaviours that reduce predation will be favoured by natural selection (Remeš 2005). For instance, nest-site choice may influence detectability or accessibility to predators (Collias & Collias 1984), reducing provisioning trips may minimise activity near nest (Skutch 1949), and active nest defence may directly deter predators (Montgomerie & Weatherhead 1988). Nest locations and behaviour modifications that reduce predation risk should be particularly important in tropical birds, where predation rates are considerably higher

compared to temperate birds (Skutch 1985; Kulesza 1990; Martin 1996; Sæther 1996).

Hiding the nest or choosing a location that is difficult for predators to locate and access is one way parents could minimise predation risk. Nest-site foliage cover may reduce the auditory, visual and olfactory cues available to potential predators (Martin 1993). Most passerines display variation in nest-site choice within populations (Filliater et al. 1994); however, the relationship between nest placement and predation is inconsistent (reviewed in Caro 2005 and Lima 2009), and appears to be influenced by many factors including life history, habitat fragmentation and predator type. Further, breeding birds may be constrained in their nest-site choices by factors such as habitat or resource availability and the presence of more

dominant individuals (Thompson 2007). In these cases, birds may compensate for nest-site effects by behaviour modification (Cresswell 1997; Muchai et al. 2001; Remeš 2005). Skutch (1949) suggested that the risk of nest predation could be amplified by increased parental activity at the nest and that this might constrain feeding rates and therefore clutch sizes. Contrary to this, many studies have shown that nest predation pressure is lower during the chick-rearing period compared to the incubation stage (Martin 1992; Martin et al. 2000b; Muchai & du Plessis 2005). Regardless of nesting stage, one way birds may reduce predation risk is to use cautious or secretive behaviours around the nest (Skutch 1949; Lima 2009).

Another way in which birds can reduce predation is through active nest defence. Polak (2013) listed potential factors influencing nest defence: sex of the parent, parental age and experience, re-nesting potential, value of the nestlings, the effectiveness of mobbing, predator distance/type and nest construction and concealment. However, it is unclear how these factors may interact in parental decision-making (Lima 2009). Mobbing predators is risky for adult birds, increasing the risk of adult mortality and injury, and depleting time and energy that would otherwise have been used elsewhere (Montgomerie & Weatherhead 1988; Filliater et al. 1994; Polak 2013). For this reason, birds should be selective about when and how they choose to defend their nest (Kleindorfer et al. 1996, 2003, 2005). While many studies have shown that active nest defence can increase the probability of fledging success (Montgomerie & Weatherhead 1988; Cresswell 1997; Olendorf & Robinson 2000), few studies have documented or quantified any detrimental effects of mobbing on parents (reviewed in Caro 2005). Ghalambor & Martin (2001) predict that tropical birds will not defend their nests as rigorously as temperate birds because tropical birds have a higher annual survival and often a longer breeding season than their temperate counterparts. Thus, they are more likely to have multiple breeding attempts, which may reduce the importance of the current nest (Ghalambor & Martin 2001; Møller & Liang 2012). Also, nest defence should be related to predator type and the ability of the parents to deter predators. For example, Patterson et al. (1980) suggested that white-crowned sparrows can do little to halt the advance of garter snakes (*Thamnophis sirtalis*), and therefore, we would expect they should invest little in nest defence against these predators. However, many studies examining the effect of nest defence on reproductive success do not differentiate between type of predator, that is mammals, reptiles or birds (Weatherhead &

Blouin-Demers 2004 but see Colombelli-Négre & Kleindorfer 2009). This may go a long way to explaining why there is little consensus on the most important factors influencing nest predation (Caro 2005).

Here, we examine the relative importance of nest-site characteristics and adult nest defence behaviours, by monitoring crimson finch (*Neochmia phaeton*) breeding success over two years across 12 sites in north-eastern Western Australia. Crimson finches are small passerines (10 g) common across northern Australia (Higgins et al. 2006). Previous work on crimson finches has shown that adult survivorship between breeding seasons is high (70–95%), pairs lay large clutches (1–7 eggs) and are multibrooded within a season (Milenkaya et al. 2011). Additionally, predation rates are often high; Milenkaya et al. (2011) found that almost 60% of clutches and 39% of young were depredated, with nearly half of the pairs in the study failing to raise a successful brood within a season. This high level of predation suggests that crimson finches are under strong selection to assess and respond to predation risk. We hypothesise that crimson finches will employ strategies to reduce predation risk, including nest-site choice (by actively selecting nest sites that are harder for predators to find/access) and active nest defence to deter predators at the nest. We also investigate whether crimson finches modify their nesting strategies in second and third nesting attempts relative to their previous experience with nest predation.

Methods

Study Species and Field Site

In total, 12 sites were monitored for nesting activity between in the East Kimberley region of Western Australia (15_340S, 128_090E) over two successive breeding seasons: January–May 2013 and January–April 2014. All sites were located near or between the towns of Wyndham and Kununurra in riparian vegetation on floodplain and/or by natural springs (three sites were only monitored in 2013, and two monitored in both years had no active nests in 2014). Adults and nestlings were banded with a numbered metal band from the Australian Bird and Bat Banding Scheme (ABBBS) and a unique combination of colour bands for individual recognition in the field (400 adults and 284 nestlings). Adult birds were aged as either in their first breeding year or older, based on both known ages and the presence of juvenile primary covert feathers (as described in Milenkaya et al. 2011). Nests were located by active searching or by

following birds back to their nests. Crimson finches do not generally form territories, and frequently build close to each other resulting in loose colonies of four to forty individuals. Previous studies found the distance between nests can be less than one metre (Milenkaya et al. 2011); however, density in this study was more dispersed with an average of 20 m between nests (range 5–100 m). Pairs commonly defend a small area directly around their nests during breeding (C. M. Young pers. obs.), and nest building is performed almost exclusively by males in riparian vegetation, predominantly *Pandanus* trees (*Pandanus spiralis*, Verbeek et al. 1993; Todd 2002; Milenkaya et al. 2011). *Pandanus* trees are palmlike structures with long rigid leaves arranged in a spiral pattern and edged with spines, each tree may have numerous stems and 'heads' of leaves (see Figures S1 and S2). Nests were checked four to five times between laying and fledging (or predation) and were considered lost to predation if all of the contents disappeared and the nest was abandoned. Daily survival was estimated using the Mayfield method (Mayfield 1975, Johnson 1979). Within the study area, *Pandanus* trees grow primarily on the floodplain and in discreet patches. 'Patches' were considered to be any number of *Pandanus* trunks stemming from a single point on the ground (as if they were a single plant). Patches were separated from the next patch by 0.5 to 100 m (\bar{x} 5.58 m, see Supplementary Material for an example of *Pandanus* habitat). Crimson finches were seen to actively defend nests against reptilian predators by producing alarm calls while hopping from perch to perch above the predator. On occasion, these calls attract the birds' partner and both birds mob the predator together. Neighbours and heterospecifics (generally other finches) attracted by mobbing calls are commonly chased off by the nest owners.

Nest Characteristics

Over the two breeding seasons, we located 182 nests (124 in 2013; 59 in 2014) and recorded the following nest-site characteristics: (i) visibility (measured as the maximum percentage of the nest that was visible from any angle); (ii) nest height (measured as metres off the ground to nearest 0.5 m); (iii) the average height of *Pandanus* trees in the patch (the mean of the highest and lowest tree measures to nearest half metre); (iv) the closest distance to another patch of *Pandanus* trees; (v) the number of *Pandanus* heads in the patch; and (vi) the presence and number of other types of vegetation (trees or shrubs) within 10 m of the nest (Fig. 1).

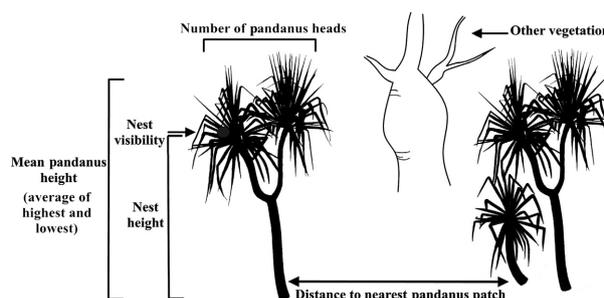


Fig. 1: An example of the nest-site characteristics measured for each nest (not to scale).

Nest Defence

A recent study by Soanes et al. (2015) found that the main nest predators of crimson finches are reptiles. Therefore, in order to gauge individual defence behaviour, we recorded the reaction of nest owners to a model of an olive python that was placed within 2 m of the nest. An olive python was chosen as a model was readily available, and a live individual had been observed in a finch nest. Birds responded in the same way to the model snake as they did to live olive pythons (C. M. Young pers. obs.), that is vocalising and moving quickly between perches close to the animal. The model snake was placed at a total of 23 crimson finch nests while the adults were absent and the response of 21 males and 17 females was recorded as they returned to their nests ($n = 23$ birds alone and 15 in pairs). Experiments were carried out in 6 of the 12 monitored sites, where the majority of breeding birds were known (banded). Just two nests had unbanded females who continually avoided capture. All presentations were made before 9:30 am and models were only placed when the bird was away from the nest. We recorded nest initiation date (date the first egg was laid) and nest stage, the number and class of any other birds present at the nest during the presentation (i.e. neighbours, one or both parents). As nesting stage is known to affect predator defence behaviour (Kleindorfer et al. 1996), we recorded stage as either eggs, young (<9 d) or old nestlings (>10 d). We chose this time as coincides with the age nestlings open their eyes (~9 d old). Observations of returning birds and their interactions with the model were recorded for 10 min, beginning when the returning bird was within the observers' visual range (due to visual obstacles to the observer over longer distances, trial recordings started around 15 m for all nests). We recorded latency to approach the model (seconds until the bird moved directly towards the

nest, within 10 m), closest approach distance (measured as distance between the bird and model) and vocalisations (total amount of time during the 10-min observation in which the bird vocalised). Based on these observations, each bird was given a response score between 1 and 6 (following, e.g. Hakkarainen et al. 1998): (i) no response, ignores the model and does not vocalise; (ii) marginal response, high latency to approach (>5 min) and few quiet vocalisations; (iii) modest response, slight delay in approach (>2 min), quiet vocalisations and moderate approach distance (1–2 m); (iv) moderate response, minimal delay in approach (~1 min), high levels of vocalisations and close approach (up to 1 m); (v) acute response, approached quickly (<30 s) with nearly constant, loud vocalisations but kept >30 cm away; (vi) extreme response, approached quickly (<30 s) with constant, loud vocalisations within 30 cm of model.

Analyses and Statistics

We analysed only those nests that we could confirm were completely depredated or successfully fledged ($n = 183$). To determine whether nesting success was different between years or across breeding stage (eggs and nestlings), we performed a chi-square analysis. All other analyses were performed using generalised linear mixed models (GLMM) with appropriate error distributions. As nests were in different breeding season and populations separated by up to 100 km, site ID and year were fitted as a random factor in all models. The first model tested the relationship between nest-site characteristics (visibility, nest height, mean *Pandanus* height, nearest *Pandanus* patch and amount of surrounding vegetation), nesting density (measured as active nests within 20 m) and nesting success (fledge/depredated, binomial). The interaction between nest height and visibility was also considered as it has been shown to be important in other studies (e.g. Colombelli-Négrel & Kleindorfer 2009). A second GLMM investigated the link between characteristics of adult birds (response score, age, sex), initiation date (date the first egg was laid) and nesting success (fledge/depredated, binomial). In the third GLMM, we determined which factors were related to adult behaviour, nest-site characteristics (from first model), nesting stage, age and sex; the dependent variable was response score (Poisson with log-link function, dispersion ratio: 0.25). Finally, we analysed the change in nest-site characteristics over sequential nesting attempts (e.g. visibility of nest 2 – visibility of nest 1) to investigate whether birds altered aspects of

their nest-site choice for subsequent nests, based on their previous experiences (fledged vs. depredated). For this, we built a binomial GLMM with the difference between nest-site characteristics as predictor variables and previous experience (fledged or failed) as the dependent variable. The ID of the nesting pair and site ID were fitted as random variables. Year was also fitted as a random variable but removed as it failed to explain any of the variance.

All analyses were run in R 3.1.2 (R Development Core Team 2014) using the packages '*lme4*' (Bates et al. 2014), '*arm*' (Gelman & Su 2014), '*AICcmodavg*' (Mazerolle 2013). All variables were standardised using '*arm*' before being put into the model. For all models, we used a backwards stepwise regression and ranked models based on Akaike's information criterion corrected for small sample size (AICc, Grueber et al. 2011; Symonds & Moussalli 2011). We calculated the differences in AICc (ΔAICc) between the best model (i.e. with the lowest AICc) and every other model and considered only models with a $\Delta\text{AICc} < 2$. To test each variable, we added it back into the final model and recalculated the AICc value.

Results

Natural Predation

Of the 182 nests observed, only 34.6% successively fledged. Daily nest survival was 0.97 across years. Predation rates were not significantly different between the two breeding seasons (2013: 67.7% depredated; 2014: 60% depredated; $\chi^2 = 0.65$, $df = 1$; $p = 0.42$). Across both years, the average incubation period was 14 ± 0.1 (SE) days (range = 11–18, $n = 97$) and the average chick-rearing period was 20 ± 0.2 (SE) days (range = 18–27, $n = 51$). Predation levels were significantly higher when there were eggs in the nest than when there were chicks (72.3% and 27.7%, respectively, $\chi^2 = 23.6$, $n = 119$, $p < 0.001$).

Nest Characteristics and Fledgling Success

Nests were more likely to successfully fledge offspring when they were further away from other patches of *Pandanus*, average height of the *Pandanus* trees in the patch was high, and nest visibility was low (Table 1; Fig. 2). The number of *Pandanus* heads in the patch, nest height and the amount of vegetation within 10 m were unrelated to nesting success. The date of the first egg was also unrelated to nest success. There was also no interaction between nest height and visibility.

Adult Behaviour, Fledgling Success and Nest Characteristics

Adult nest defence behaviour was unrelated to nest success ($n = 38$ Table 2a). Adult behaviour was also unrelated to the age and sex of the adult birds, initiation date, nesting stage and nesting density. Similarly, there was no relationship between nest defence behaviour and the height of the nest, nest visibility, mean height of the *Pandanus* patch, the number of *Pandanus* heads within the patch, the distance to the nearest *Pandanus* patch or the amount of other vegetation within 10 m ($n = 38$, Table 2b).

Change in Nest-site Choice

Birds that had more than one nesting attempt during the breeding season did not select a nest site that was characteristically different from their previous site, regardless of whether previous nesting attempt was depredated or successful ($n = 32$, Table 2c).

Discussion

Nest Characteristics and Fledgling Success

The probability of nest success was shown to be strongly related to multiple aspects of the nest site: its visibility, the mean height of the surrounding vegetation and its isolation. Essentially, nests that were more difficult for predators to locate or access were more likely to survive to fledging. Although these factors have been recognised as important in previous studies (reviewed in Caro 2005 and Lima 2009), they seem to be population dependent. For example, a study of red-backed shrikes (*Lanius collurio*) in Switzerland found that less visible nests were more successful (Müller et al. 2005), while a similar study on the same species in Poland found no influence of nest concealment on predation (Goławski & Mitrus 2008). Likewise, a recent study by Soanes et al. (2015) found that predation rates on another population of crimson finches were

unaffected by nest-site characteristics including visibility and vegetation structure. One potential explanation for the discrepancy between our study population and that of Soanes et al. (2015) is the difference in vegetation structure and predation risks (as well as predator species) between sites. While Soanes et al. (2015) focused on a population in a very dense habitat, our study focused on populations breeding on flood plains, with patchy and dispersed vegetation. It is likely that this variation in habitat structure affects not only variation in nest-site choice, but also the composition of the predator community. Soanes et al. (2015) identified the primary crimson finch nest predators to be water monitors (*Varanus mitchelli* and *Varanus mer-tensi*), Gilbert's dragons (*Lophognathus gilberti*) and water pythons (*Liasis fuscus*); however, water pythons and water monitors were not present at our sites. Instead, the main predators in our study area are likely to be olive pythons (*Liasis olivaceus*), Gilbert's dragons and freckled monitors (*Varanus tristis*). During the current study, one predation event by an olive python was observed, and crimson finches were observed mobbing all three species on at least six other occasions (C. M. Young pers. obs.). It is unlikely that reptiles are the only nest predators in the area. Corvids and raptors were seen; however, we found no evidence that they entered the *Pandanus* and are more likely to be a threat to adults than to eggs or nestlings. Finally, we attributed one predation event to a mammal, as parts of chicks were found in the nest (see Best 1978).

Population difference in vegetation structure and the predator community could influence the effectiveness of predator search techniques (i.e. olfaction vs. visual), which could alter the risks associated with various nest-site choices and behaviours (Caro 2005). For example, nest visibility may be more important in open habitat than in closed, while distance between vegetation patches would become negligible in dense habitat. Reptiles are known to use both visual and olfactory senses to detect prey (Burghardt 1970; Cooper 1988; Kotler et al. 1992); therefore, a greater distance between *Pandanus* patches may mask odour trails making it harder for reptiles to detect nests. This could reduce the profitability of a potentially risky crossing through open areas to get to new patches. Kleindorfer et al. (2003) found that nest defence towards a model snake was greatest by nests that were more exposed from underneath, suggesting that nest visibility can be an important factor in predation by reptiles, that is also recognised by some birds. As we

Table 1: Nest characteristics and nest success (fledged/failed). The top model (by >2 AICc) predicting the success of nests ($n = 182$)

	Estimate	SE	p Value
Intercept	-0.68	0.17	<0.01
Mean <i>Pandanus</i> height	0.84	0.36	0.02
Nearest <i>Pandanus</i>	1.28	0.56	0.02
Visibility	-0.77	0.33	0.02

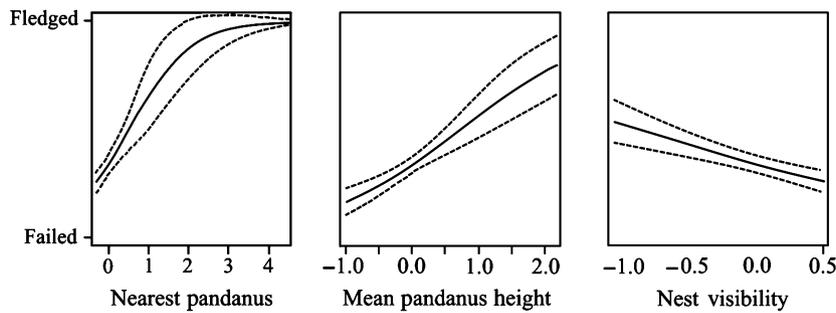


Fig. 2: Predicted values (from the top model) examining which nest-site characteristics are significantly related to nest success. Solid lines are predicted values based on the model; broken lines indicate standard error.

Table 2: Relationships between a) nest defence behaviour and nesting success ($n = 38$), b) nest defence behaviour and nest-site characteristics ($n = 38$), c) previous nesting success and subsequent nest-site choice ($n = 32$). Top two models for each GLMM shown. In all cases, the top model was <2 AICc's different from the null model and all variables were non-significant

Model	Variable	Coefficient	SE	p	AICc	Δ AICc
(a) Behaviour and success						
1	Response score	2.18	1.24	0.08	44.94	0
2	Null	–	–	–	45.26	0.32
(b) Vegetation and behaviour						
1	Null	–	–	–	140.37	0
2	Nearest <i>Pandanus</i>	0.17	0.15	0.25	141.65	1.28
(c) Previous experience and second nest site						
1	Null	–	–	–	44.16	0
2	Mean <i>Pandanus</i> height	–1.01	0.99	0.31	45.73	1.57

could not disentangle nesting density (number of nests within 20 m) from distance to the closest *Pandanus*, we cannot rule out the possibility that predators are simply attracted to areas with more nests. Nests that were located in *Pandanus* with a higher mean vegetation height were also more likely to survive, although nest height (metres above the ground) within the patch was not related to success. This suggests that the actual structure of the vegetation was important rather than the nests position within it. Higher vegetation may allow chicks to detect vibrations from predators sooner, giving chicks more time to escape (Stake et al. 2005).

Alternately patches with vegetation lower on the ground might be more attractive to predators by providing easier and quicker access to cover.

Adult Behaviour and Fledging Success

It has been suggested that birds can reduce predation using active defence to deter nest predators (Mont-

gomerie & Weatherhead 1988). However, we found no evidence that crimson finches displaying higher aggression towards the model of a nest predator were more likely to successfully fledge young. This result is consistent with Soanes et al. (2015) that also noted that crimson finches do not appear to be effective in active nest defence against reptilian predators. They found that predation rates of active nests were comparable to that of experimental nests, suggesting that parents were unable to successfully defend nests (Soanes et al. 2015). Many smaller birds, which may otherwise have ineffective defence mechanisms against predators, may engage in collaborative mobbing, discouraging predators through group harassment (Flasskamp 1994). In our study, mobbing calls rarely attracted attention even from the individual's partner (8/38 mobbing calls attracted another bird). On occasion, other species were attracted (commonly other finches) and they were chased off by the nest owner. Further, although small birds can successfully deter some types of nest predators through active nest defence (e.g. Knight & Temple 1988; Kleindorfer et al. 2003; Grim 2008), it is unclear how effective birds can be against reptilian predators, even when they defend as a group. There is evidence that reptiles can locate nests by observing parental activity and parents may hence adapt their behaviour to reduce predation risk (Skutch 1949; Lawler 1989; Lima & Dill 1990; Sih et al. 1992; Lima 1998; Martin et al. 2000a,b). However, as found by Milenkaya et al. (2011) and Soanes et al. (2015), most crimson finch nests in this study were depredated at the egg stage, rather than the nestling stage when adult activity at the nest is higher. Although Stake et al. (2005) found that snake predation was more prevalent in the late chick stage, early nest stage predation is common across species in many studies, reporting that once nests survived to hatching, they were likely to fledge successfully (review Martin 1992; also see Roper & Goldstein 1997; Muchai & du Plessis 2005). Rompré & Robinson (2008) found that preda-

tion on neotropical antbird nests by snakes most frequently occurred in the first week of incubation. Other possible explanations are that nests that make it to the nestling stage are simply higher quality, that is built in areas that naturally have less predators, so are less likely to be depredated. Additionally, we found no effect of nesting stage on defensive behaviour. Although not unheard of (e.g. Dale et al. 1996), this is unusual in birds (reviewed in Caro 2005). It is possible that this lack of effect was a result of limited sample size in this study. However, it is possible that adult crimson finches defend all stages of nesting equally if there is little cost to the adult in doing so.

Nest-site Characteristics and Adult Behaviour

We found no link between nest-site characteristics and adult defence behaviour, meaning birds that nested in more predator prone sites did not display higher aggression towards nest predators. It is not always clear whether birds can perceive predation risk and modify their behaviour or nesting decisions accordingly (Muchai & du Plessis 2005). Despite this, many studies have suggested that birds should and can compensate for a lack of vegetation cover by modifying their behaviour (Møller 1989; Cresswell 1997; Muchai et al. 2001). In one example, Kleindorfer et al. (2005) found that warblers could differentiate between predator threat levels and defended more vigorously against snakes at low nests than they did hawks. It therefore seems likely that crimson finches either do not accurately assess predation risk (in the ways we have measured), or are simply limited in their ability to defend their nests from local predators.

Change in Nest-site Choice

If crimson finches were able to assess and respond to predation risk, we predicted that (after a predation event) birds would build subsequent nests in positions less prone to predation. Although parents always built a new nest for subsequent attempts, we found no relationship between previous experience and nest-site selection. Pairs that had previously experienced nest predation were not more likely to select a nest site that was less visible, further from other *Pandanus*, or in *Pandanus* with a greater mean height for their second or third attempt. One possibility for the failure to utilise a different (potentially more successful) nest sites is that birds may be limited in access to these sites by

the presence of more dominant individuals, however, as we did not find an influence of pair identity on nest success this seems unlikely. An alternative explanation is that there are trade-offs associated with nest-site selection. Factors that provide a safe nesting site, such as low visibility, may also have poorer microclimates for eggs and chicks, or pose a higher risk to parents (Caro 2005). For example, parents may build more exposed nests so they are able to scan their surroundings and have time to escape any predators that may be present (Caro 2005). Crimson finches are relatively long lived (>5 yr) with high adult survival rates (Milenkaya et al. 2011), and this combination of life-history traits may lead them to value their own survival and future reproductive value over their current nesting attempt (Schmidt & Whelan 2010).

Conclusion

Despite finding that isolation, visibility and mean vegetation height all had a positive influence in nesting success; crimson finches did not alter/improve these aspects of nest-site choices after a predation event. While birds did engage in active nest defence against a model predator, the strength of their defence was unrelated to nest stage (e.g. incubation of eggs or feeding chicks) and subsequent nesting success. It is also possible that by choosing to nest in the hostile *Pandanus* vegetation (with long rigid leaves, edged with spines), crimson finches are already limiting predation by making nests inaccessible to a wider range of predators. To date, much of the work on nest predation avoidance has been conducted on temperate species, where the primary nest predators are mammals or other birds. Perhaps as a consequence, little is known about how effective nest defence of small birds is against reptilian predators. Reptiles, particularly snakes, may be harder for nesting birds to detect than avian or mammalian predators (Misenhelter & Rotenberry 2000; Godard et al. 2007). Roper (2005) suggested that, rather than investing in predation avoidance, tropical birds should use multiple nesting attempts, within and between seasons, as a way of dealing with high nest predation pressures. This study reveals that although nest-site choice can positively influence nesting success in crimson finches, adult birds do not alter their choice of sites in response to predation events. Instead, they appear to use multiple nesting attempts to overcome the high predation pressure.

Acknowledgements

This work was supported by Australian Research Council Grants (S.R.P), an A.N.U PhD scholarship (C.M.Y) and a Fund for Avian Research grant from The Australian Bird Study Association (C.M.Y). We thank Fiona Finch and Sophie Keats for help in the field as well as Save The Gouldian Fund for providing access to their field station. We are grateful to David Hamilton and reviewers for helpful comments on the manuscript, Thomas Merklung and Liam Bailey for assistance with R software. All work was approved by the Australian National University's Animal Ethics Committee (A2012/55).

Literature Cited

- Bates, D., Maechler, M., Bolker, B. & Walker, S. 2014: lme4: Linear mixed-effects models using Eigen and S4. R package version 1.1-7
- Best, L. B. 1978: Field Sparrow reproductive success and nesting ecology. *Auk* **95**, 9—22.
- Burghardt, G. M. 1970: Chemical perception in reptiles. In: *Advances in Chemoreception, Vol. I. Communication by Chemical Signals* (Johnston, J. W., Moulton, D. G. & Turk, A., eds). Appleton-Century-Crofts, New York, NY, USA, pp. 241—308.
- Caro, T. 2005: *Antipredator Defences in Birds and Mammals*. The University of Chicago Press, Chicago, IL, USA.
- Collias, N. E. & Collias, E. C. 1984: *Nest Building and Bird Behavior*. Princeton Univ. Press, Princeton, NJ, USA.
- Colombelli-Négrel, D. & Kleindorfer, S. 2009: Nest height, nest concealment, and predator type predict nest predation in superb fairy-wrens (*Malurus cyaneus*). *Ecol. Res.* **24**, 921—928.
- Cooper, W. E. J. 1988: Prey odor discrimination in the varanoid lizards *Heloderma suspectum* and *Varanus exanthematicus*. *Ethology* **81**, 250—258.
- Cresswell, W. 1997: Nest predation: the relative effects of nest characteristics, clutch size and parental behaviour. *Anim. Behav.* **53**, 93—103.
- Dale, S., Gustavsen, R. & Slagsvold, T. 1996: Risk taking during parental care: a test of three hypotheses applied to the pied flycatcher. *Behavioral Ecology and Sociobiology* **39**, 31—42.
- Filliater, T. S., Breitwisch, R. & Nealen, P. M. 1994: Predation on Northern cardinal nests: does choice of nest site matter? *Condor* **96**, 761—768.
- Flasskamp, A. 1994: The adaptive significance of avian mobbing v. an experimental tests of the 'move on' hypothesis. *Ethology* **96**, 322—333.
- Gelman, A. & Su, Y. 2014: arm: data analysis using regression and multilevel/hierarchical models. R package version 1.7-07.
- Ghalambor, C. K. & Martin, T. E. 2001: Fecundity-survival trade-offs and parental risk-taking in birds. *Science* **292**, 494.
- Godard, R. D., Bowers, B. B. & Wilson, C. M. 2007: Eastern bluebirds *Sialis sialis*, do not avoid nest boxes with chemical cues from two common nest predators. *J. Avian Biol.* **38**, 128—131.
- Golawski, A. & Mitrus, C. 2008: What is more important: nest-site concealment or aggressive behaviour? A case study of the red-backed shrike, *Lanius collurio*. *Folia Zool.* **57**, 403—410.
- Grim, T. 2008: Are Blackcaps (*Sylvia atricapilla*) defending their nests also calling for help from their neighbours? *J. Ornithol.* **149**, 169—180.
- Grueber, C. E., Nakagawa, S., Laws, R. J. & Jamieson, I. G. 2011: Multimodel inference in ecology and evolution: challenges and solutions. *J. Evol. Biol.* **24**, 699—711.
- Hakkarainen, H., Ilmonen, P., Koivunen, V. & Korpimäki, E. 1998: Blood parasites and nest defense behaviour of Tengmalm's owls. *Oecologia* **114**, 574—577.
- Higgins, P. J., Peter, J. M. & Cowling, S. J. 2006: *Handbook of Australian, New Zealand and Antarctic Birds. Vol. 7: Boatbill to Starlings*. Oxford Univ. Press, Melbourne, Vic., Australia.
- Kleindorfer, S., Hoi, H. & Fessl, B. 1996: Alarm calls and chick reactions in the moustached warbler, *Acrocephalus melanopogon*. *Anim. Behav.* **51**, 1199—1206.
- Kleindorfer, S., Fessl, B. & Hoi, H. 2003: The role of nest site cover for parental nest defence and fledging success in two *Acrocephalus* warblers. *Avian Sci.* **3**, 21—29.
- Kleindorfer, S., Fessl, B. & Hoi, H. 2005: Avian nest defence behaviour: assessment in relation to predator distance and type and nest height. *Anim. Behav.* **69**, 307—313.
- Knight, R. L. & Temple, S. A. 1988: Nest-defense behavior in the red-winged blackbird. *Condor* **90**, 193—200.
- Kotler, B. P., Blaustein, L. & Brown, J. S. 1992: Predator facilitation: the combined effect of snakes and owls on the foraging behavior of gerbils. *Ann. Zool. Fenn.* **29**, 199—206.
- Kulesza, G. 1990: An analysis of clutch-size in New World passerine birds. *Ibis* **132**, 407—422.
- Lawler, S. P. 1989: Behavioral responses to predators and predation risk in four species of larval anurans. *Anim. Behav.* **38**, 1039—1047.
- Lima, S. L. 1998: Stress and decision making under the risk of predation: recent developments from behavioral, reproductive, and ecological perspectives. *Adv. Study Behav.* **27**, 215—290.
- Lima, S. L. 2009: Predators and the breeding bird: behavioural and reproductive flexibility under the risk of predation. *Biol. Rev.* **84**, 485—513.
- Lima, S. L. & Dill, L. M. 1990: Behavioral decisions made under the risk of predation: a review and prospectus. *Can. J. Zool.* **68**, 619—640.

- Martin, T. E. 1992: Breeding productivity considerations: what are the appropriate habitat features for management? In: *Ecology and Conservation of Neotropical Migrant Landbirds* (Hagan, J. M. & Johnstone, D. W., eds). Smithsonian Institution Press, Washington, DC, USA, pp. 455–473.
- Martin, T. E. 1993: Nest predation and nest sites: new perspectives on old patterns. *Bioscience* **43**, 523–532.
- Martin, T. E. 1996: Life history evolution in tropical and south temperate birds: what do we really know? *J. Avian Biol.* **27**, 263–273.
- Martin, T. E. & Clobert, J. 1996: Nest predation and avian life-history evolution in Europe versus North America: a possible role of humans? *Am. Nat.* **147**, 1028–1046.
- Martin, T. E., Martin, P. R., Olson, C. R., Heidinger, B. J. & Fontaine, J. J. 2000a: Parental care and clutch sizes in North and South American birds. *Science* **287**, 1482–1485.
- Martin, T. E., Scott, J. & Menge, C. 2000b: Nest predation increases with parental activity: separating nest site and parental activity effects. *Proc. R. Soc. Lond. B* **267**, 2287–2293.
- Mazerolle, M. J. 2013: AICcmodavg: model selection and multimodel inference based on (Q)AIC(c). R package version 1.35.
- Milenkaya, O., Legge, S. & Walters, J. R. 2011: Breeding biology and life-history traits of an Australasian tropical granivore, the Crimson Finch (*Neochmia phaeton*). *Emu* **111**, 312–320.
- Misenhelter, M. D. & Rotenberry, J. T. 2000: Choices and consequences of habitat occupancy and nest site selection in sage sparrows. *Ecology* **81**, 2892–2901.
- Møller, A. P. 1989: Nest predation selects for small nest size in the blackbird. *Oikos* **57**, 237–240.
- Møller, A. P. & Liang, W. 2012: Tropical birds take small risks. *Behav. Ecol.* **24**, 267–272.
- Montgomerie, R. D. & Weatherhead, P. J. 1988: Risks and rewards of nest defence by parent birds. *Q. Rev. Biol.* **63**, 167–187.
- Muchai, M. & du Plessis, M. A. 2005: Nest predation of grassland bird species increases with parental activity at the nest. *J. Avian Biol.* **36**, 110–116.
- Muchai, M., Bennun, L. A. & Lens, L. 2001: Notes on the behaviour and ecology of Sharpe's longclaw, a threatened Kenyan grassland endemic. *Scopus* **22**, 23–28.
- Müller, M., Pasinelli, G., Schiegg, K., Spaar, R. & Jenni, L. 2005: Ecological and social effects on reproduction and local recruitment in the red-backed shrike. *Oecologia* **143**, 37–50.
- Olendorf, R. & Robinson, S. K. 2000: Effectiveness of nest defence in the Acadian flycatcher *Empidonax vireescens*. *Ibis* **142**, 365–371.
- Patterson, T. L., Petrinovich, L. & James, D. K. 1980: Reproductive value and appropriateness of response to predators by White-crowned Sparrows. *Behav. Ecol. Sociobiol.* **7**, 227–231.
- Polak, M. 2013: Comparison of nest defence behaviour between two associate passerines. *J. Ethol.* **31**, 1–7.
- R Development Core Team 2014: R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria.
- Remes, V. 2005: Nest concealment and parental behaviour interact in affecting nest survival in the blackcap (*Sylvia atricapilla*): an experimental evaluation of the parental compensation hypothesis. *Behav. Ecol. Sociobiol.* **58**, 326–333.
- Ricklefs, R. E. 1969: An analysis of nesting mortality in birds. *Smithson. Contrib. Zool.* **9**, 1–48.
- Rompré, G. & Robinson, W. D. 2008: Predation, nest attendance, and long incubation periods of two neotropical antbirds. *Ecotropica* **14**, 81–87.
- Roper, J. 2005: Try and try again: nest predation favours persistence in a neotropical bird. *Ornitol. Neotrop.* **16**, 253–262.
- Roper, J. J. & Goldstein, R. R. 1997: A test of the Skutch hypothesis: does activity at nests increase nest predation risk? *J. Avian Biol.* **28**, 111–116.
- Sæther, B. E. 1996: Evolution of avian life-histories – does nest predation explain it all?. *Trends Ecol. Evol.* **11**, 311–312.
- Schmidt, K. A. & Whelan, C. J. 2010: Nesting in an uncertain world: information and sampling the future. *Oikos* **119**, 245–253.
- Sih, A., Kats, L. B. & Moore, R. D. 1992: Effects of predatory sunfish on the density, drift and refuge use of stream salamander larvae. *Ecology* **73**, 1418–1430.
- Skutch, A. F. 1949: Do tropical birds rear as many young as they can nourish? *Ibis* **91**, 430–455.
- Skutch, A. F. 1985: Clutch size, nesting success, and predation on nests of Neotropical birds, reviewed. *Ornithol. Monogr.* **36**, 575–594.
- Soanes, R., Peters, A., Delhey, K. & Doody, J. S. 2015: The Influence of Nest Site Choice and Predator Sensory Cues on Nest Success in the Crimson Finch, *Neochmia phaeton*. *Emu* doi.org/10.1071/MU14046.
- Stake, M. M., Thompson, F. R. III, Faaborg, J. & Burhans, D. E. 2005: Patterns of snake predation at songbird nests in Missouri and Texas. *J. Herpetol.* **39**, 215–222.
- Symonds, M. R. E. & Moussalli, A. 2011: A brief guide to model selection, multimodel inference and model averaging in behavioural ecology using Akaike's information criterion. *Behav. Ecol. Sociobiol.* **65**, 13–21.
- Thompson, F. R. 2007: Factors affecting nest predation on forest songbirds in North America. *Ibis* **149**, 98–109.

- Todd, M. K. 2002: Nest-site and breeding-season data for the Crimson Finch *Nechmia phaeton* in Australia. *Aust. Bird Watcher* **19**, 161—171.
- Verbeek, N. A. M., Braithwaite, R. W. & Boasson, R. 1993: The importance of *Pandanus spiralis* to bird. *Emu* **93**, 53—58.
- Weatherhead, P. J. & Blouin-Demers, G. 2004: Understanding Avian nest predation: why ornithologists should study snakes. *J. Avian Biol.* **35**, 185—190.

Supporting Information

Additional supporting information may be found in the online version of this article:

Figure S1: An example of typical *Pandanus* habitat in the study site.

Figure S2: Close up of the nest of a crimson finch nest from Figure S1. This is a typical crimson finch nest built between two rows of *Pandanus* leaves.